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SPACING AND PHYSICAL HABITAT SELECTION PATTERNS OF PEREGRINE FALCONS IN CENTRAL WEST GREENLAND

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ABSTRACT.—We examined nest-site spacing and selection of nesting cliffs by Peregrine Falcons (*Falco peregrinus*) in central West Greenland. Our sample included 67 nesting cliffs that were occupied at least once between 1972 and 1999 and 38 cliffs with no known history of Peregrine Falcon occupancy. We measured 29 eyrie, cliff, and topographical features at each occupied nesting cliff and unused cliff in 1998–1999 and used them to model the probability of peregrines occupying a cliff for a breeding attempt. Nearest-neighbor distance was significantly greater than both nearest-cliff distance and nearest-occupied distance (the distance between an occupied cliff and one occupied at least once, 1972–1999). Thus, spacing among occupied cliffs was probably the most important factor limiting nesting-cliff availability, and, ultimately, peregrine nesting densities. Although some unused cliffs were unavailable in a given year because of peregrine spacing behavior, physical characteristics apparently made some cliffs unsuitable, regardless of availability. We confirmed the importance of several features common to descriptions of peregrine nesting habitat and found that peregrines occupied tall nesting cliffs with open views. They chose nesting cliffs with eyrie ledges that provided a moderate degree of overhang protection and that were inaccessible to ground predators. Overall, we concluded that certain features of a cliff were important in determining its suitability as a nest site, but within a given breeding season there also must be sufficient spacing between neighboring falcon pairs. Our habitat model and information on spacing requirements may be applicable to other areas of Greenland and the Arctic, and can be used to test the generalities about features of Peregrine Falcon nesting cliffs throughout the species' widespread distribution. *Received 31 March 2004, accepted 18 March 2005.*

Habitat selection is the process by which an animal chooses suitable habitats (Manly et al. 1993, Litvaitis et al. 1994), and can be measured when an animal uses a resource disproportionately to its availability (Johnson 1980). Features of the habitat that are important for occupancy can function as meaningful indicators of habitat selection, even when the amount of available habitat is unknown (Manly et al. 1993). Historically, many researchers have studied Peregrine Falcons (*Falco peregrinus*; hereafter peregrine) in conjunction with the decline of populations caused by DDT in the mid-1900s (Cade et al. 1988), and there have been many descriptions of peregrine nesting habitat (e.g., White and Cade 1971, Court et al. 1987, Emison et al. 1997). However, there have been only two studies in which there were quantitative tests of habitat features that influence habitat selection, and both studies occurred in temperate regions (Grebence and White 1989, Gainzarain et al. 2000). There are no such quantitative data for arctic environments, and there is little information on habitat characteristics that appear to be universal across the species' extensive distribution. Although Peregrine Falcons are described as intolerant of nesting pairs nearby (Cade 1960, Ratcliffe 1993), there have been no tests to evaluate the importance of spacing between suitable nesting cliffs or nearest neighbors. Gainzarain et al. (2000) calculated an average distance between nesting cliffs occupied by Peregrine Falcons, but this permitted only a general prediction of habitat use and was not a reflection of actual spacing. Availability of a nesting cliff may depend on the distribution of occupied nesting cliffs, which may vary among years (Ratcliffe 1993).

The two most important factors limiting raptor densities are the availability of physical nesting habitat or food, whichever is in shorter supply (Hickey 1942, Newton 1979). Newton (1998) suggested that nest-site availability can be limiting for species with specialized nesting-cliff requirements. Because peregrines

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prey opportunistically on many different bird species, the population trend of any one species usually does not affect peregrine breeding densities (Hickey 1942). In central West Greenland, most of the falcon's diet comprises four passerine species (Rosenfield et al. 1995); within 400 m of peregrine eyries, densities of these species are reduced, but they are abundant 400 to 3,000 m from the eyrie and at random locations on the study area tundra (Meese and Fuller 1989). Although peregrines may hunt regularly within 1,500 m of nesting cliffs (Tucker et al. 2000), some may travel 20–43 km on hunting flights (Enderson and Craig 1997). Newton (1998) suggested that food availability near nests is not important to species that forage elsewhere. Thus, nesting-cliff availability may be a more important limiting factor than local prey availability. Because of our limited knowledge of peregrine breeding biology in the Arctic and the importance of nesting-cliff availability, we investigated habitat selection and spacing as potential factors limiting peregrine nesting densities.

The migratory arctic Peregrine Falcon (Tundra Peregrine Falcon, *F. p. tundrius*) breeds in regions of Canada, Alaska, and the ice-free portion of Greenland (Cade et al. 1988, White et al. 2002). Since 1972, participants in the Greenland Peregrine Falcon Survey (GPFS) have routinely surveyed for breeding arctic peregrines in central West Greenland (Mattox and Seegar 1988). On the initial search, GPFS surveyors found only nine pairs of peregrines occupying cliffs. By 1999, there were 133 known peregrine nesting cliffs in the study area (W. G. Mattox unpubl. data). The 28 years of data collected on this population made it ideal for studying relationships between nesting-cliff occupancy, spacing, and physical habitat characteristics. Our objectives were (1) to determine whether availability of nesting cliffs was limited, (2) to evaluate whether unused cliffs were unsuitable or unavailable for occupancy because of peregrine spacing requirements, and (3) to determine which habitat characteristics may be important for peregrine nesting-cliff selection.

METHODS

Study area.—We conducted our study in the Kangerlussuaq region of central West Greenland, which encompasses one of the widest portions of ice-free land on the island. The study area, delineated by W. G. Mattox and colleagues in 1972, is approximately 2,500 km^2 in area and lies between 66° 45′ N and 67° 15′ N (Mattox and Seegar 1988). Søndre Strømfjord—the longest fjord in West Greenland—divides the area, which extends approximately 100 km from the inland ice cap almost to the western coast. Elevations range from sea level to 1,120 m, and summer temperatures usually range between 0 and 15° C. Located in a belt of short, arctic vegetation, the landscape is dominated by willow scrub (*Salix glauca*), dwarf birch (*Betula nana*), lichens, mosses, sedges, and grasses (Böcher et al. 1968) interspersed with many ponds and lakes.

Definitions.—We defined an *eyrie* as the place on a ledge where a falcon lays her eggs (Ratcliffe 1993). We used the term *nesting cliff* to define a topographic feature containing one or more eyries or potential eyries, but occupied by only one pair of peregrines in a given year. Alternative nesting cliffs may occur within the range of one mated pair of birds. Rock faces and knolls were typically discrete topographic features in our study area and there was little continuous cliff habitat; thus, nesting cliffs were discrete features and did not overlap. *Availability* is the presence and accessibility of the habitat, or habitat feature, and is generally subject to the biological and social constraints of that species, which includes intra- and interspecific competition (Johnson 1980). Gyrfalcons (*F. rusticolus*) and Common Ravens (*Corvus corax*; hereafter ravens) were the only other common cliff-nesting species and only potential nest-site competitors. Gyrfalcons and ravens occupied nesting cliffs prior to the arrival of peregrines in the spring (W. G. Mattox pers. comm.), possibly influencing peregrine selection of nesting cliffs. Occupancy of nesting cliffs by Gyrfalcons varied widely among years and nesting cliffs (W. G. Mattox unpubl. data). In any year, Gyrfalcons and ravens combined occupied up to 8% of peregrine nesting cliffs and peregrines nested on up to 33% of nesting cliffs already occupied by either of these two species (W. G. Mattox unpubl. data). Therefore, the potential for interspecific competition for nesting cliffs was relatively low, and we assumed that all nesting cliffs were available to peregrines at some time between 1972 and 1999. We classified a nesting cliff as *occupied* if we or other GPFS members observed a pair of peregrines at the nesting cliff during the breeding season (June–August) in any year from 1972 to 1999. The majority of these occupancies represented egg-laying attempts, but in a few cases adult pairs occupied nesting cliffs for several seasons without producing eggs (W. G. Mattox unpubl. data). We defined an *unused* cliff as any cliff where there was no known history or evidence of occupancy from 1972 to 1999. We considered only unused cliffs that had at least 14 m of vertical rock face because the shortest occupied cliff in the study area was 14 m in height. Our sample consisted of 105 cliffs; 67 were occupied and 38 were unused.

Habitat measures.—In the summers of 1998 and 1999, we measured nesting-cliff characteristics. Due to logistical constraints, we could not completely randomize our sample of nesting cliffs, but we measured all occupied and unused nesting cliffs encountered along or near portions of six survey routes established by the GPFS. Our sample of 105 cliffs constitutes approximately 50% of known cliffs in the study area, and the proportion of occupied to unused cliffs was likely representative of the total study area. Thus, despite a non-random sample, our estimate of nesting-cliff selection is meaningful, even when the standard error of features may not reflect the true variation in the total population of cliffs (Manly et al. 1993). For a complete description of GPFS survey methods, see Burnham and Mattox (1984).

We measured three features of nesting-cliff distribution by plotting all cliffs on a topographic map and measuring the linear distance between cliffs. The *nearest cliff* was the cliff closest to the sample cliff (n = 67 occupied, n = 38 unused), whether or not peregrines had ever occupied it. The *nearest occupied cliff* was the nearest nesting cliff occupied by peregrines at any time between 1972 and 1999. We measured the distance to the nearest cliff and the nearest occupied cliff from occupied and unused cliffs. We defined the third spatial measure, distance to *nearest neighbor,* as the distance to the nearest nesting cliff occupied by peregrines in the same breeding season as the sampled nesting cliff. Because unused cliffs cannot have neighbors, we recorded this measure for occupied sites only. If the nearest-neighbor distance for a given nesting cliff varied among years, then we used the shortest distance recorded between 1972 and 1999.

We measured physical features of nesting cliffs at the three spatial levels: eyrie ledge, cliff, and surrounding topography. We measured 26 characteristics in addition to the three spacing features (Appendix) based on results from previous studies. A team of at least two persons hiked to cliffs and climbed to eyries and unused ledges to measure and record data. At occupied nesting cliffs, we measured the eyrie ledge used most recently. At unused nesting cliffs, we selected one ledge as a putative eyrie to measure. All measured ledges at unused nesting cliffs were flat (~0° slope) and at least large enough to accommodate a scrape for eggs. Although our selection of unused ledges was subjective, we attempted to select the ledge that provided the best combination of protection from predators and humans (Mearns and Newton 1988) and microclimatic benefits (Falk et al. 1986).

Analyses.—Because data deviated from normality, we used a nonparametric Wilcoxon matched-pairs signed rank test to compare among measures of spatial distribution for each occupied nesting cliff (Zar 1996). Comparisons between nearest-neighbor and nearest-cliff distances, and between nearest-neighbor and nearest-occupied cliff distances were not independent of one another, so we used a Bonferroni adjusted alpha of 0.025 to control for inflated type I errors.

To test for nonrandom orientation, we conducted Rayleigh's test of circular uniformity on aspect data for occupied and unused nesting cliffs (Zar 1996). Parametric tests for circular data assume the data are from a von Mises distribution, which is the circular equivalent to a normal distribution. As our data did not always meet the assumption for a parametric test, we used a nonparametric procedure for unimodal data that compared the mean direction of occupied and unused nesting cliffs against a chi-square distribution (Fisher 1993:116, Method P). This nonparametric procedure allowed us to evaluate whether or not cliff and eyrie ledge aspect were important in peregrine nesting-cliff selection.

We used logistic regression to predict the probability of occupancy according to habitat features. Three habitat features—nearest-neighbor distance and cliff and ledge aspect—were not included in our logistic regression analysis because we could not calculate a value for unused cliffs (nearest neighbor) or the data were circular (aspect data) and could not be used appropriately in a linear analysis. Collinearity of predictor variables in linear or logistic regression can cause unexpected regression coefficients or large standard errors; thus, it was necessary to delete one or more intercorrelated variables before conducting our analysis (Hosmer and Lemeshow 1989, Zar 1996). We retained only one of a pair of correlated variables ($r \geq 0.60$) that were easier to measure or that have been shown to be important features of peregrine nesting-cliff habitat elsewhere. We also eliminated one variable (slope) that we were unable to measure at all nesting cliffs. We eliminated 8 of 26 variables (eyrie height, cliff height at eyrie, elevation of cliff above the drainage, nearest cliff, elevation of cliff, length of ledge, overhang categories, and slope), retaining 18 for analysis.

With the 18 retained variables, we used the best subsets variable-selection technique to determine which variables to include in a logistic regression analysis and chose the combination of habitat variables that produced the best C(p) Mallow statistic (Hosmer and Lemeshow 1989). This technique provided all possible pairings among habitat variables and identified which combinations of variables provided the best fit to the data. We tested for the importance of interactions between certain habitat features in this variable selection step. Then, we used the combination of habitat variables identified as providing the best fit to the data in a logistic regression to predict the probability of occupancy (Hosmer and Lemeshow 1989, Allison 1999). We modeled the probability of each cliff being assigned to an occupied nesting cliff (1) as opposed to an unused cliff (0) based on habitat features. We evaluated the fit and the predictive power of the logistic regression model using the Hosmer-Lemeshow goodness-of-fit test ($\hat{C}$) and the max-rescaled r-square value, respectively. We used SAS software (SAS Institute, Inc. 1990) to conduct analyses and assigned a significance level of alpha equal to 0.05.

RESULTS

The nearest-neighbor distance of 67 occupied sites was significantly greater than its paired, nearest-cliff distance ($T_{0.05(2),67} = 333$, $n = 67$, $P < 0.001$). Nearest-neighbor distance was also significantly greater than its paired, nearest-occupied cliff distance ($T_{0.05(2),67} = 52$, $n = 67$, $P < 0.001$).

We measured circular, linear, and categorical (Tables 1 and 2) habitat features at nesting cliffs that were occupied ($n = 67$) and unused ($n = 38$). Cliff aspect at occupied and unused nesting cliffs ($Z_{0.05,67} = 26.25$, $P < 0.001$; $Z_{0.05,38} = 12.67$, $P < 0.001$, respectively) and on eyrie ledges or unused ledges ($Z_{0.05,59} = 18.66$, $P < 0.001$; $Z_{0.05,34} = 10.24$, $P < 0.001$, respectively) was significantly oriented to the south. Mean orientation did not differ between occupied and unused cliffs ($\chi^2 = 0.07$, $n = 105$, $P = 0.79$) or between used or unused ledges ($\chi^2 = 0.28$, $n = 93$, $P = 0.60$).

The best subset variable-reduction technique identified five variables important in modeling nesting-cliff occupancy by peregrines (Table 3) and the slope of the logistic regression line was significantly different from zero ($G_5 = 38.52$, $n = 76$, $P < 0.001$). Our logistic regression model was effective for describing occupied sites ($\hat{C}_8 = 5.91$, $P = 0.66$) and had moderate predictive power (rescaled $r^2 = 0.54$). The adjusted odds ratio for each variable in the model indicates the effect of each variable on the probability of occupancy at a cliff. An odds ratio of 0.967 for vertical angle of exposure indicated that there is a 3.3% increase in odds of occupancy with every 1-degree decrease in exposure. Odds of occupancy increased by 89.3% if ledges were inaccessible to predators and by 96.7% if the ledge substrate was sand or dirt, rather than a stick nest. For every 1 m increase in cliff height and 1 m decrease in elevation of hill across valley, odds of occupancy increased by 1.7% and 0.7%, respectively.

DISCUSSION

Spacing among occupied nesting cliffs was an important component of cliff occupancy in our study. Our results suggest that some near-

TABLE 1. Physical characteristics of 67 occupied and 38 unused cliffs measured to evaluate Peregrine Falcon nesting-cliff selection in central West Greenland. Measurements were made in 1998–1999; cliffs were categorized as occupied or unused based on their occupancy history from 1972 to 1999.[a]

	Occupied			Unused		
Physical features	n^b	Mean ± SE	Range	n^b	Mean ± SE	Range
Eyrie characteristics						
Length of eyrie ledge (cm)	57	686.2 ± 152	50–6,089	28	234.7 ± 31.0	52–600
Depth of eyrie ledge (cm)	57	164.7 ± 32.7	17–1,500	28	105.4 ± 11.3	21–274
Eyrie aspect (°)	67	188.7 ± 0.9	15–345	34	195.1 ± 81.5	65–292
Horizontal angle of exposure (°)	49	144.4 ± 4.8	54–205	30	144.9 ± 8.4	65–236
Vertical angle of exposure (°)	48	65.2 ± 2.8	25–110	29	84.0 ± 6.4	20–150
Cliff characteristics						
Elevation of cliff (m)	67	288.0 ± 14.1	100–550	38	265.1 ± 20.1	75–550
Cliff height (m)	67	98.8 ± 8.0	14–365	38	61.0 ± 5.3	14–147
Height of hill below cliff (m)	67	39.8 ± 4.1	0–138	38	53.3 ± 7.7	0–198
Slope (m)	57	1.70 ± 0.11	0.71–5.08	32	1.34 ± 0.16	0.09–5.19
Cliff aspect (°)	67	187.7 ± 0.8	21–360	38	190.5 ± 1.3	20–330
Height of eyrie ledge (m)	65	51.1 ± 5.4	5–224	35	24.8 ± 3.2	7–78
Cliff height at eyrie ledge (m)	65	94.3 ± 8.2	14–365	35	52.2 ± 5.7	14–154
Topographical characteristics						
Distance to permanent water (m)	67	452.7 ± 55.4	0–2,750	38	561.3 ± 81.9	0–2,500
Elevation gain within 3-km radius (m)	67	205.2 ± 11.3	50–475	38	179.6 ± 14.4	25–500
Elevation of cliff above drainage (m)	67	161.4 ± 10.8	26–450	38	130.9 ± 11.5	25–300
Distance to drainage (m)	67	577.9 ± 72.4	0–2,250	38	643.8 ± 84.1	0–2,000
Elevation of hill across valley (m)	67	348.6 ± 14.0	125–600	38	399.4 ± 26.9	125–750
Distance to hill across valley (km)	67	2.19 ± 0.14	0.3–5.0	38	2.6 ± 0.2	0.5–6.5
Distance to nearest cliff (km)	67	2.16 ± 0.14	0.2–5.0	38	1.4 ± 0.1	0.2–3.3
Distance to nearest occupied cliff (km)	67	2.69 ± 0.13	0.3–5.1	38	2.1 ± 0.2	0.2–5.0
Distance to nearest neighbor (km)	67	3.27 ± 0.18	1.3–11.2		N/A	

[a] See Appendix for definition of habitat features.
[b] At a few nesting cliffs and unused cliffs, we were unable to access or could not identify the eyrie or unused ledge. Thus, our sample size for eyrie characteristics or location varies from 67 occupied nesting cliffs and 38 unused cliffs. We also could not calculate slope of cliff if we could not measure accurately the distance from the observer to the top of the cliff.

est nesting cliffs, occupied at least once and, thus, suitable, are not available in some years due to their proximity to a site already occupied by peregrines. Therefore, availability of a particular nest site may vary among years depending on the current distribution of occupied nesting cliffs. Dispersion among animal-use areas can result from a variety of causes, including competition for food or nesting resources (Fretwell and Lucas 1969, Newton 1998). Intraspecific aggression of peregrines has been noted at nest sites (Ratcliffe 1993, White et al. 2002), and spacing requirements may be a mechanism for reducing the costs associated with agonistic behavior.

Unused nesting cliffs also may not be available in every year because of peregrine spacing requirements. However, we can assume that unused cliffs were available for occupancy at some time between 1972 and 1999 be-

TABLE 2. Categorical habitat features measured at 67 occupied nesting cliffs and 38 cliffs unused by Peregrine Falcons to evaluate habitat selection in central West Greenland. Measurements were made in 1998–1999; cliffs were categorized as occupied or unused based on their occupancy history from 1972 to 1999.[a]

Physical features	Occupied[b]	%	Unused[b]	%
Ledge characteristics				
Overhang protection on ledge				
None	6	11%	15	47%
Slight	10	18%	6	19%
Partial	29	54%	5	16%
Complete	9	17%	6	19%
Accessible to predation				
Yes	16	28%	15	47%
No	42	72%	17	53%
Substrate at or near scrape				
Sand or dirt	44	81%	11	38%
Moss	0	0%	3	10%
Vegetation	6	11%	9	31%
Gravel	1	2%	2	7%
Stick nest	2	4%	4	14%
Bare rock	1	2%	0	0%
Vegetation on ledge				
Yes	42	74%	22	65%
No	15	26%	12	35%
Cliff characteristics				
Vegetation at base of cliff				
Willow-steppe mix	21	33%	18	47%
Heath-willow mix	18	28%	14	37%
Heath-steppe mix	8	13%	3	8%
Herbslope	5	8%	0	0%
Water	4	6%	1	3%
Willow copse	8	13%	2	5%
Boulders at base of cliff				
Yes	57	89%	25	66%
No	7	11%	13	34%
Position of ledge on cliff				
Lower	15	24%	9	20%
Middle	30	48%	31	69%
Upper	18	29%	5	11%
Human disturbance				
Minimal	57	85%	33	87%
Moderate	9	13%	5	13%
Severe	1	1%	0	0%

[a] See Appendix for definition of terms.

[b] At a few nesting cliffs and unused cliffs, we were unable to access or could not identify the eyrie or unused ledge. Thus, our sample size for eyrie characteristics or placement varies from 67 occupied nesting cliffs and 38 unused cliffs.

cause no nesting cliff was occupied in each of the last 28 years (peregrines occupied nesting cliffs 20–96% of years checked after the nesting cliff was located), and breeding pairs moved up to 3.5 km among years to alternative nesting cliffs (W. G. Mattox unpubl. data). Spacing of cliffs was also not important in our logistic regression model predicting nesting-cliff occupancy. Thus, some unused nesting cliffs are probably unsuitable regardless of their availability because they do not contain features important for peregrine nesting.

The eyrie ledge features that we identified

TABLE 3. Peregrine Falcons in central West Greenland selected tall nesting cliffs with prominent views and eyrie ledges that provided protection from weather and predators. Our logistic regression model predicts the probability of a cliff being occupied by peregrines using habitat features measured at 48 occupied nesting cliffs (1) and 28 unused cliffs (0). Negative coefficients (β) indicate a negative association between that variable and cliff occupancy. Habitat variables included in our model were selected using the best subset variable-selection technique. Measurements were made in 1998–1999; cliffs were categorized as occupied or unused based on their occupancy history from 1972 to 1999.[a]

Variable[b]	β	SE	Wald χ^2	df	P[c]	exp(β)[d]	95% Wald	CL
Intercept	5.715	1.808	9.99	1	0.002	—	—	—
Vertical angle of exposure	−0.034	0.015	5.37	1	0.020	0.967	0.939	0.995
Accessibility of ledge	−2.239	0.765	8.56	1	0.003	0.107	0.024	0.478
Stick nest on ledge	−3.413	1.231	7.68	1	0.006	0.033	0.003	0.368
Cliff height	0.017	0.007	5.56	1	0.020	1.017	1.003	1.032
Elevation of hill across valley	−0.008	0.003	8.13	1	0.004	0.992	0.987	0.998

[a] We were unable to measure all eyrie and ledge characteristics at all cliffs because of accessibility problems. Our sample for the logistic regression model is lower than our complete sample of 67 occupied nesting cliffs and 38 unused cliffs because it includes only those cliffs where all five habitat variables were measured.

[b] See Appendix for definition of terms.

[c] P-values based on Wald χ^2 statistic.

[d] Odds ratios indicate the change in odds of occupancy for each unit change of the variable. For example, the odds ratio for elevation of hill across the valley is 0.992. This means that for each 1 m decrease in elevation the odds of occupancy increase by 0.8%. Accessibility of ledge and stick nest on ledge are binary variables; thus, the odds ratios reflect 89.3% and 96.7% increases in odds of occupancy, respectively, if the ledges are not accessible (by foxes or humans) or there is not a stick nest on the ledge.

as being important in nesting-cliff occupancy suggest that peregrines choose nesting sites with ledges that provide microclimatic benefits and protection from predators. Eyrie ledges that afford protection from weather are associated with occupancy by peregrines throughout North America (Cade 1960, Falk et al. 1986, Court et al. 1988). Bradley et al. (1997) found that mean clutch size of peregrines in subarctic Canada decreased with greater precipitation and that nestling mortality increased with annual precipitation during storms. This suggests that microclimate of the eyrie, influenced by vertical protection of the overhang above the ledge, may be an important feature in nesting-cliff occupancy by peregrines.

Approximately one-third of peregrine eyries in Great Britain were on raven stick nests (Ratcliffe 1993) and, in Alaska, 20% nested on Rough-legged Hawk (*Buteo lagopus*) stick nests (Cade 1960). Thus, stick nests can provide a suitable substrate for peregrine eyries. Ravens in our study area began nesting in early May and tended to build their stick nests under rock overhangs that completely shaded the ledge (CSW pers. obs.). The negative association we found between nesting-cliff occupancy and stick nests may represent selection for moderate, rather than complete, overhang protection on the ledge. Moderate overhang protection would provide some protection from weather, but also allow peregrines to receive warmth from the arctic sun. Most cliffs were oriented to the south and therefore were positioned to take advantage of solar insolation. Our results support those of Burnham and Mattox (1984), who suggested that peregrines in central West Greenland choose eyrie ledges that balance solar exploitation and protection from weather.

Peregrine nesting cliffs in several regions of the world are associated with tall, dominant cliffs that provide a commanding outlook (Hickey 1942, Grebence and White 1989, Gainzarain et al. 2000). Jenkins and Hockey (2001) proposed a latitudinal gradient in cliff height, suggesting that peregrines occupied low cliffs in arctic regions (mean cliff height <10 m at 65° latitude). Our data, however, indicate that peregrines will choose tall cliffs with commanding views, if available, in arctic areas, as well. Tall cliffs and open views apparently benefit peregrines by providing better perches for hunting or defense from intruders (Mearns and Newton 1988, Ratcliffe 1993, Jenkins 2000). Jenkins (2000) documented greater hunting success from perches at nesting cliffs than from aerial hunts, and he found a positive relationship between hunting success and tall cliffs. However, in our study area the primary prey of peregrines were ground nesting and foraging passerines (Rosenfield et al. 1995), which suggests that the contour-hugging, surprise attack behavior described by White and Nelson (1991) may be a more effective strategy for capturing prey than aerial attacks from cliffs. Thus, the benefits of defense from conspecifics and predators (e.g., arctic fox, *Alopex lagopus*), rather than enhanced foraging opportunities provided by tall nesting cliffs with commanding views, are probably more influential in nesting-cliff selection. We conclude that competition plays an important role in nesting-cliff suitability, as well as availability.

We identified features that were limited in availability but important for nesting-cliff selection by peregrines. However, certain features important in habitat selection may be abundant in our study area and, therefore, our methods may not have allowed us to identify these features. For instance, Cade (1960), Ellis (1982), and Court et al. (1988) found that peregrine nesting cliffs often were close to water. Surface water provides a place for peregrines to bathe and good habitat for some of their prey (Cade 1960). However, we found no association between occupied nesting cliffs and distance to water. There is an abundance of small lakes and streams in our study area, so water is generally found close to all cliffs (mean = 492.0 m ± 46.2 SE, range = 0–2,750 m).

Of the many habitat features we measured, we found five that characterized occupancy by peregrines. Nesting cliffs may be suitable to peregrines by meeting just a few critical spatial and habitat requirements. This adaptability in nest-site selection may contribute to the worldwide distribution of peregrines. Spacing, and thus availability, of suitable breeding sites is probably the most important proximate factor limiting the nesting densities of peregrines in our study area. Characteristics of the nesting cliff are important for determining the suitability of a nesting cliff if there is sufficient space between neighbors to accommodate a breeding attempt in a given year. Our results suggest that peregrines select tall nesting cliffs with commanding views and protected ledges for nest-defense and microclimatic benefits. The similarities of nesting-cliff features at occupied peregrine nesting cliffs among geographic regions suggest that our predictive model of nesting-cliff occupancy—using physical characteristics and peregrine spacing requirements—could be applicable to other areas of Greenland and the Arctic.

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APPENDIX. Description of physical characteristics measured at 67 occupied nesting cliffs and 38 cliffs unused by Peregrine Falcons in central West Greenland. Measurements were made in 1998–1999; cliffs were categorized as occupied or unused based on their occupancy history from 1972 to 1999.

Feature	Description	Method
Cliff features[a]		
Elevation (m)	Meters above sea level at top of cliff	Topographic map
Cliff height (m)	Cliff height from base of cliff to highest point, not including any ledges or tiers	Rangefinder and clinometer[b]
Slope (m)	Slope of cliff calculated as rise/run	Rangefinder and clinometer[c]
Height of hill below cliff (m)	Measured from base of hill to bottom of cliff formation	Rangefinder and clinometer[b]
Aspect of cliff (°)	Aspect perpendicular to rock face	Compass
Vegetation	Predominant vegetation types below cliff face	Direct observation
Boulders	Presence of boulders at base of cliff	Direct observation
Height of ledge (m)	Height from base of cliff to ledge	Rangefinder and clinometer[b]
Height of cliff at ledge (m)	Cliff height intersecting ledge	Rangefinder and clinometer[b]
Position of ledge on cliff	Upper, center, lower and right, middle, left	Direct observation
Human disturbance	Minimal: >5 km from human settlement or roads Moderate: 1–5 km from human settlements or roads Severe: <1 km from human settlements or roads	Topographic map
Ledge features[d]		
Ledge length (cm)	Length of ledge at longest point	Measuring tape
Ledge depth (cm)	Depth of ledge at widest point	Measuring tape
Aspect of ledge (°)	Aspect of ledge perpendicular to back wall	Compass
Horizontal angle of exposure (°)	Degree of opening to right and to left of ledge	Compass
Vertical angle of exposure (°)	Back wall of ledge to front lip of roof at ledge	Clinometer
Accessible by fox or human	Yes or no	Direct observation
Substrate material on ledge	Bare rock, gravel, sand/dirt, vegetation, or stick nest	Direct observation
Vegetation on ledge	Yes or no	Direct observation
Overhang protection on ledge	None: 0% of ledge shaded midday Slight: 1–25% of ledge shaded midday Partial: 50–75% of ledge shaded midday Complete: ledge completely shaded midday	Direct observation
Topographical features		
Total elevation gain (m)	Elevation of cliff minus lowest elevation within a 3-km radius circle around nesting cliff	Topographic map
Elevation above drainage (m)	Elevation of cliff minus elevation of drainage	Topographic map
Elevation of hill across valley (m)	Elevation of hills across valley from cliff	Topographic map
Distance to permanent water (m)	Distance from cliff to permanent water	Topographic map
Distance to drainage (m)	Distance from sample cliff to closest drainage	Topographic map
Distance to hills across valley (km)	Distance from cliff to hills across valley	Topographic map
Nearest cliff (km)	Distance from sample cliff to nearest cliff regardless of occupancy status	Topographic map

APPENDIX. Continued.

Feature	Description	Method
Nearest occupied cliff (km)	Distance from sample cliff to nearest cliff occupied by peregrines at least once between 1972 and 1999	Historical data and topographic map
Nearest neighbor (km)	Distance from sample cliff to nearest cliff occupied in same year	Historical data and topographic map

[a] Continuous vertical rock >14 m tall surrounding the eyrie or putative eyrie.

[b] All cliffs were level with or higher than the observation point. Height was measured by calculating the height to the top and bottom of the cliff from the observation point (e.g., distance to top × sin [angle to top]) and then subtracting the bottom height from the top height. For a few tall cliffs, we were unable to measure the distance to the top of the cliff. To measure height at these cliffs, we used the equation: height = a × b, where a = the angle to bottom of cliff × angle to top of cliff, and b = distance to bottom of cliff × secant from observation point to bottom of cliff.

[c] Slope could not be calculated at those cliffs where we could not measure the distance to the top of the cliff because the horizontal distance of the cliff (run) was unknown at these sites.

[d] Place on ledge where eggs laid. On unused ledges, measures were taken from the best potential eyrie ledge (i.e., 0° slope).